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Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea

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ABSTRACT: Spatial and temporal variability in environmental factors can exert major influences on survival and growth of living organisms. However, in many key areas of fisheries science (e.g. growth, survival and recruitment determination), environmental heterogeneity is usually ignored because of insufficient environmental or fisheries data or lack of evidence that such heterogeneity impacts response variables. For the eastern Baltic Sea (ICES Subdivisions 25 to 32), we evaluated spatial and temporal differences in conditions affecting the survival of cod *Gadus morhua* L. eggs at survival on four distinct spawning sites within the assessment area. We intercalibrated ways of quantifying the volume of water ('reproductive volume') at each site where salinity, oxygen and temperature conditions permitted successful egg development. We have developed and compared a time series (1952 to 1996) of reproductive volumes among the areas to identify spatial differences. The results of 2 independent volume-estimation methods are comparable, indicating that highly significant differences exist among the sites, and that the westernmost spawning ground, Bornholm Basin, has on average the highest reproductive volume and the lowest variability among the 4 sites. These findings may be useful in evaluating how spatial and temporal variability in environmental conditions affect egg hatching success and possibly recruitment in the Baltic stock.

KEY WORDS: Baltic Sea · Cod eggs · Environmental heterogeneity · Oxygen · Survival · Spatial distributions

INTRODUCTION

The cod *Gadus morhua* L. population in the eastern Baltic Sea is confronted with a set of environmental conditions which differ from those experienced by populations in all other geographic areas. Here cod eggs are neutrally buoyant in relatively deep water (>50 m deep; salinity 10 to 15 psu) due to the low salinity of the surface layer (6 to 8 psu). In contrast, cod eggs in other areas, where surface salinities are typically >28 psu, are neutrally buoyant in the upper 20 to 50 m (e.g. Kjesbu et al. 1997). As a result cod eggs in the Baltic have a vertical distribution which is concentrated in deep water and usually near or below the permanent halocline (Grauman 1984, Wieland & Jarre-Teichmann 1997, Wlodarczyk & Horbowa 1997).

This vertical distribution frequently results in cod eggs being exposed to water with a very low oxygen concentration (e.g. Nissling et al. 1994, Wieland et al. 1994). Water masses in the deep parts of the Baltic basins are situated below a permanent halocline that greatly inhibits the role of vertical mixing in renewing oxygen levels in the deep layers (Stigebrandt 1987). As a result, oxygen levels below the halocline can become extremely low due to aerobic metabolism and the

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decomposition of organic matter sinking from the surface layer (Stigebrandt & Wulff 1987).

The main process which can reverse this situation is the occasional inflow of oxygen-rich waters from the North Sea (Matthäus & Franck 1992). In the absence of such inflows, oxygen concentrations below the halocline progressively decrease to <2 ml^{-1}, concentrations at which no Baltic cod eggs will develop and hatch successfully (Wieland et al. 1994). As a result the thickness of the layer of water ('spawning layer': Plikshs et al. 1993) with suitable salinity and oxygen conditions decreases until no water remains in which successful egg development can take place. In the Baltic, areas most remote from the influence of North Sea inflows tend to be most susceptible to anoxic conditions in the deep layers (HELCOM 1996). Hence there are often strong spatial gradients (horizontally and vertically) in oxygen conditions within the Baltic Proper.

It has been widely believed among Baltic fisheries scientists and oceanographers for many years that such interactions are critical for successful reproduction and a prerequisite for strong year-classes (e.g. Grauman 1973, Kosior & Netzel 1989, Bagge et al. 1994, Helcom 1996, Schnack et al. 1996, ICES 1998). However, in order to evaluate this hypothesis statistically, it would be helpful if the volume of water suitable for cod egg development could be quantified. This volume of water (called the 'reproductive volume' by Plikshs et al. 1993) would effectively represent a measure of habitat size for this particular life-history stage.

In an initial attempt to quantify habitat size for cod eggs in the Baltic, Plikshs et al. (1993) estimated reproductive volumes at each of the 4 main spawning sites (see Fig. 1), i.e. the Bornholm Basin, the Gdansk Deep, and the southern and the central Gotland Basin, in different months for the years 1952 to 1992. Volumes were estimated by horizontally integrating the spawning-layer thickness estimated at a single central hydrographic station across the area of each basin. Their time series indicate that volumes varied greatly between the 4 basins and between years. In addition, they found statistical evidence that recruitment was positively related to total reproductive volume (after allowing for spawning stock biomass), and 2 subsequent studies using the same reproductive volume data but a different recruitment time series obtained a similar result (Sparholt 1996, Jarre-Teichman et al. in press).

In the future, such studies may not be possible because hydrographic sampling efforts changed during the 1990s. The Latvian time series in the Bornholm and Gdansk Basins stopped in 1992, but has continued in the Gotland Basin (Plikshs pers. comm.). A new historical time series for the Bornholm Basin has been constructed by the University of Kiel (Hinrichsen & Wieland 1996) and is being continued (Hinrichsen

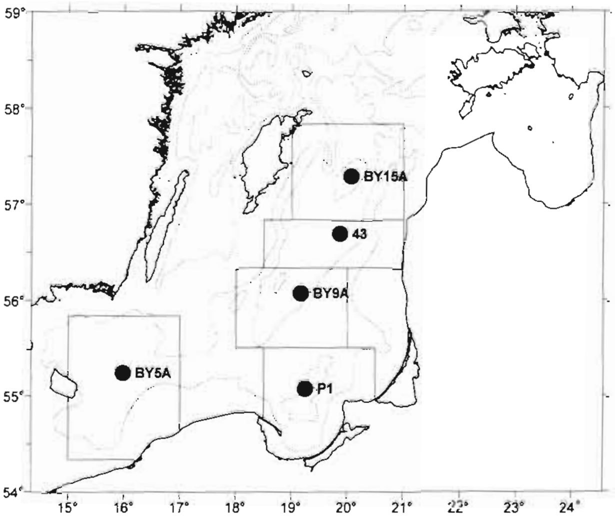

Fig. 1. Map of Baltic Sea showing locations of hydrographic sampling sites (●) and boxes within which reproductive volumes were calculated by Plikshs et al. (1993). Stns BY5A, P1, BY9A, 43, and BY15A are located in Bornholm Basin, Gdansk Basin, southern Gotland Basin and central Gotland Basin (Stns 43 and BY15A), respectively

pers. comm.); however the Kiel measurements are being compiled by different methods (e.g. more stations per basin) and hydrographic data than the Latvian estimates. Moreover, the Kiel measurements do not provide information about conditions in the Gdansk and Gotland Basins. Russian investigators have been developing estimates of reproductive volume in the Gdansk and southern Gotland Basins (Feldman et al. 1996, Zezera & Zezera 1997) using a methodology similar to that of Plikshs et al. (1993), but using multiple hydrographic stations per basin. The changes in sampling effort and methods mean that it may no longer be possible to obtain a complete and unbiased representation of conditions in all areas for all years.

In this paper, we compare and intercalibrate the methodologies for volume estimation so that new series can be developed and used in future modelling studies (e.g recruitment, eutrophication). First, we present a full description of these methodologies, characterise some of the main statistical features of the reproductive volume distributions, and evaluate the degree of spatial variability between spawning areas. Second, we evaluate the hypothesis that 1 hydrographic station is sufficient to represent a whole basin for the purpose of estimating its reproductive volume. This hypothesis was evaluated because all of the reproductive volume data used in previous recruitment-modelling exercises (Plikshs et al. 1993, Sparholt 1996) were based on 1 hydrographic station per spawning area, even though various types of mesoscale horizontal and vertical motions (e.g. inflows from Arkona basin and areas to the west, coastal upwelling, internal waves) could affect hydrographic conditions in some areas of a given basin but not elsewhere within the same basin (Zezera & Zezera 1997).

METHODS

Reproductive volumes were estimated in different ways and with different data sources by 2 institutes. The sequence of data collection, processing, calibration and comparison is described in detail in the following subsections.

Estimation methodology of Latvian Fisheries Research Institute (LatFRI). Reproductive volume estimates derived by LatFRI (Plikshs et al. 1993) employed a contouring program ('Balthypsograph' prepared by Wulff and Andersson, University of Stockholm; details below) to estimate a volume of water whose hydrographic conditions were considered suitable for the development of cod *Gadus morhua* eggs, i.e. all water with a salinity of >11 psu and an oxygen concentration of >2 ml^{-1}. These criteria were based on studies which established how interactions between cod-egg buoyancy, vertical distibution and oxygen concentration affect survival of cod eggs in the Baltic (Grauman 1973, Nissling & Westin 1991, Bagge et al. 1994).

The hydrographic input data for the contouring program were collected at 1 site in the deepest part of each of the deep basins of the Baltic (Fig. 1). These sites were considered by Plikshs et al. (1993) to constitute only a rough approximation of conditions elsewhere in each basin, but they did allow estimates of reproductive volume to be calculated for long periods since the stations are frequently visited as part of various national and international monitoring programs.

The contouring software used for the volume estimations employs the hypsographic function for the Baltic proper derived from a gridded 5' × 5' bathymetric database by Stigebrandt (1987) and Stigebrandt & Wulff (1987). This function quantifies the volumes of water below horizontal surfaces at given depth levels. The depth levels at which horizontal surfaces are chosen for calculating water volumes are defined by the vertical profile of hydrographic data collected at the station in the basin. Hence, the volume of water between any 2 surfaces (e.g. those represented by the 11 psu and 2 ml^{-1} oxygen levels) can be derived by assuming horizontal homogeneity on a basin-wide scale.

Estimates were made for various months of the year for the period 1952 to 1992 for all 4 basins; in addition, estimates are available for the southern and central Gotland Basin for the years 1993 to 1996. The raw hydrographic data used as input for the calculations by LatFRI represents national data collected by this institute during all years from 1960 to present date. These data have not been deposited in international databases, e.g. International Council for the Exploration of the Sea (ICES) and the (HELCOM). For the years 1952 to 1959, published ICES data from the annual volumes of *Annales Biologiques* and *Bulletin Hydrographique* were used for the Bornholm Basin and southern Gotland Basin calculations, data in Glowinska (1963) were used for the Gdansk Basin calculations, and the former USSR's *Sea Hydrometeorological Annals (Baltic Sea)* were used as the data source for the central Gotland Basin. The time series for the Gdansk Basin was extended beyond 1992 using data collected by Feldman et al. (1996) for the years 1993 and 1994.

Estimation methodology of Institute of Marine Science (IfMK). The hydrographic data set consists of measurements from 16 cruises carried out in the Bornholm Basin between May 1989 and April 1996 (Hinrichsen & Wieland 1996). The station grid represents the Bornholm Basin enclosed by the 60 m isobath (Fig. 2). Two cruises conducted in 1989 covered only 21 stations, while during all other surveys 36 standard stations were covered with a mean horizontal resolution of ~10 n miles. The survey data were used to calculate the thickness of the spawning layer of Baltic cod, i.e. the vertical extension of the water body considered suitable for successful egg development (salinity >11 psu, oxygen >2 ml^{-1}, temperature >1.5°C). These are the threshold levels for salinity and oxygen content derived in the previous subsection; a lower temperature boundary was considered in addition since low temperature limits the upper boundary of the water column suitable for egg development in years following severe winters (Wieland & Jarre-Teichmann 1997).

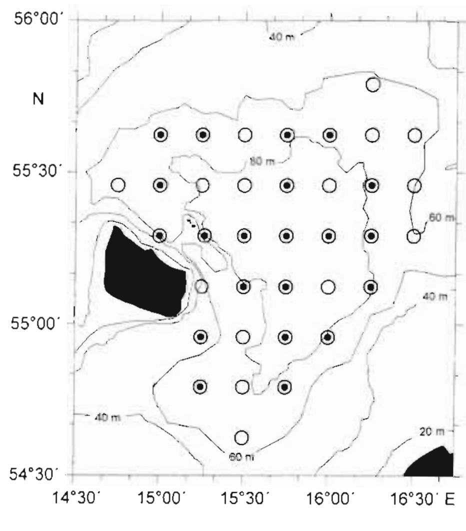

Fig. 2. Grid of hydrographic stations in Bornholm Basin used by University of Kiel research vessels for determining reproductive volumes during years 1989 (●: 21 stations) and 1991–1996 (○: 36 stations)

Horizontal fields of the thickness of the spawning layer were constructed by objective analysis (Bretherton et al. 1976) based on a standard statistical approach — the Gauss-Markov theorem — which yields an expression for the linear least-square error estimate of the variables. Objective analysis has the advantage that it can make use of statistical results (spatial covariance function of measurements) and assumptions concerning measurement noise and small-scale errors inferred from the observed data. Thus, at every single point an estimate can be given that depends linearly on the total number of measurements, i.e. a weighted sum of all observations (Bretherton et al. 1976). Objective analysis provides a smoothed version of the original measurements, with a tendency to underestimate the true field because of the specific assumptions involved in our treatment of measurement noise and small-scale signals unresolved by the observation array. Error estimates depend only on the statistics of the field, the noise level, and on the locations of the observation points, and not the measurements themselves. Hence, error maps can be calculated *a priori* for different array designs without reference to any particular data set.

As most of the experiments between 1989 and 1996 were designed to produce synoptic maps of the spawning layer, an accurate mapping technique was required. Applying the technique of objective analysis, a unit array configuration with $d\lambda = 2'$ and $d\varphi = 1'$ (horizontal resolution = ~1.8 km) was provided based on the standard station-grid, whereby each grid point is representative of the thickness of the spawning layer centered around it. It was assumed that the error variance due to measurement errors and small-scale noise amounted to 15% of the total variance of the field. The reproductive volume of Baltic cod in the entire study area was calculated for the different surveys by simple horizontal integration of the fields of the thickness of the spawning layer, whereby only the area for which the expected root-mean-square (rms) error in the interpolation amounted to less than 20% was considered. The 20% rms error line was chosen because it is closely related to the 60 m isobath that corresponds to the horizontal limit of the cod egg distribution (Wieland 1995, Wieland & Horbowa 1996).

For each of the 36 stations, the thickness of the spawning layer was compared with the total reproductive volume obtained for the 14 observation dates in the period 1991 to 1996 using linear regression analysis. To take into account reproductive volumes representing the extremely bad environmental conditions observed during the stagnation period in the late 1980s, data from the 2 additional surveys (1989, based on a 21 station grid: Fig. 2) were included in the analysis. The reproductive volumes for 1989 were estimated with reference to the unit array configuration based on the standard grid (36 stations).

Additional vertical profiles of salinity and temperature were obtained from the ICES hydrographic database for the period 1958 to 1996. With these data, a time series of reproductive volumes was constructed using the relationship between single-point measurements of the thickness of the spawning layer in the central Bornholm Basin (HELCOM Stn BY5: Fig. 1) and the basin-wide estimates of the reproductive volume for the years 1989 and 1991 to 1996.

Data analyses. Each time series of reproductive volume was plotted to enable visual inspection of the raw data (Appendix 1; these data will also be available later in 2000 from http://www.ifm.uni-kiel.de/fi/STORE/welcome.htm). Frequency distributions were compared between areas, and 2-way analyses of variance were conducted to compare differences in reproductive volume between basins and months.

Intercomparison of 2 reproductive volume time series developed for Bornholm Basin. The 2 methodologies outlined in the first 2 subsections differ substantially in terms of approach, number of stations per basin, and source of the raw hydrographic data. If existing Latvian estimates are to be combined with new Kiel measurements to derive new time series for the Bornholm Basin, or for the entire Baltic, it is necessary that the series be comparable and, if necessary, appropriate calibrations applied. We compared the 2 reproductive volume series for the Bornholm Basin directly by regressing estimates from one series against the other on a month-specific basis and for all months combined. The years covered by this analysis were 1958 to 1992. If the 2 series are directly comparable, the slope and intercept for these regression models should equal 1 and 0, respectively, and the explained variation (R^2) should be highly significant ($p < 0.05$). Deviations from the expected slope and intercept values indicate bias of one series relative to the other. We used the output regression models to update the Bornholm Basin time series prepared by Plikshs et al. (1993) and fill in missing data points.

RESULTS

Overall statistical characteristics and between-basin spatial differences

The time series of reproductive volume in each of the basins show wide (10- to 20-fold) multi-year variability (Fig. 3). The site with the largest and least variable reproductive volume (in terms of coefficient of variation, SD/mean) was the Bornholm Basin (Table 1). The most variable site was the central Gotland Basin. The frequency distributions of all observations recorded in all

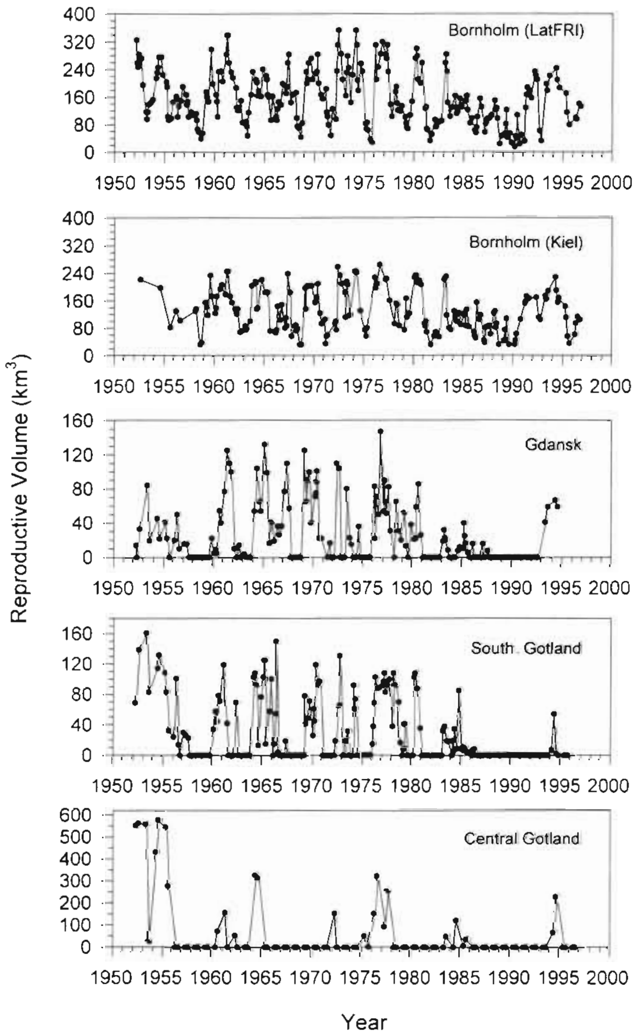

Fig. 3. Time series of reproductive volumes for each spawning site. 2 series of estimates for the Bornholm Basin were prepared by Plikshs et al. (1993: LatFRI [LatFRI: Latvian Fisheries Institute]) and Hinrichsen & Wieland (1996: Kiel). Time series for the other basins were prepared by Pliksbs et al. (1993); however, Gdansk Basin data from 1993 onwards were estimated semi-quantitatively from contour plots of Feldman et al. (1996)

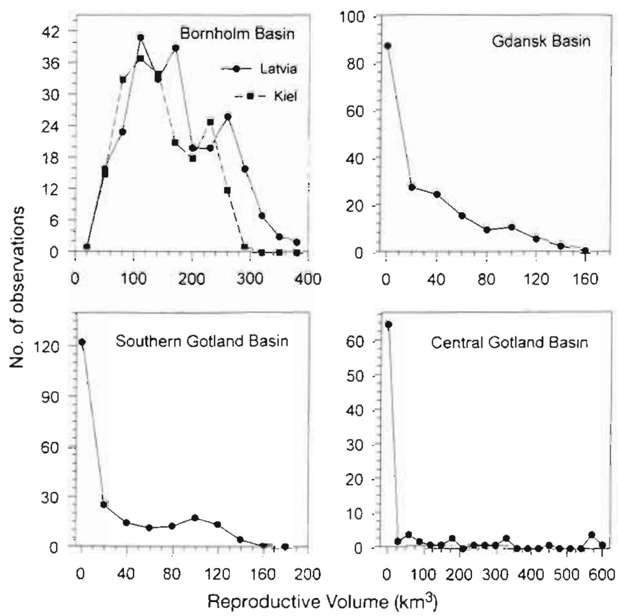

Fig. 4. Frequency distributions of reproductive volumes in each of the 4 deep basins of the Baltic Sea. Time periods covered by data and summary statistics are given in Table 1

months at each of the sites show that 3 of the 4 series are skewed towards zero (Fig. 4). Median values in the 2 northeasternmost basins were zero (Table 1).

Two-way ANOVA (main effects: basin and month) revealed basin to be the dominant effect. The basin effect explained 60% of the variance in reproductive volumes ($p < 0.0001$) for the months when data were available for only the Bornholm, Gdansk and southern Gotland basins; the month effect was insignificant ($p = 0.61$). During the months when data were available for the Central Gotland Basin (May and August), the basin effect explained 23% of the variance in reproductive volume ($p < 0.0001$) and the month effect was insignificant ($p = 0.28$). In both cases, the Bornholm Basin had the highest mean reproductive volume ($p > 0.05$; GT2 multiple-comparison test: SAS Institute Inc.

Table 1. Summary statistics of raw reproductive volume (km^3) data for each main spawning basin of cod *Gadus morhua* in central Baltic Sea. LatFRI: Latvian Fisheries Research Institute; AtlantNIRO: Atlantic Scientific Research Institute of Marine Fisheries and Oceanography

Basin	Time period	N	Mean (SD)	Median
Bornholm (LatFRI)	1952–1992	246	158 (78)	147
Bornholm(Kiel)	1958–1996	197	130 (62)	122
Gdansk (LatFRI & AtlantNIRO)	1952–1994	187	25 (35)	8.5
Southern Gotland (LatFRI)	1952–1995	228	28 (41)	0
Central Gotland (LatFRI)	1952–1996	90	66 (149)	0

Table 2. Total mean (SE) reproductive volume (Vol) in Baltic Sea and mean (SE) monthly proportion in Bornholm Basin (Bornholm %) during 1952 to 1992. Data are LatFRI estimates. May and August data include central Gotland Basin, which is excluded from results for other months. (N for May and August: number of years when measurements available for all basins; N for other months: number of years when data available for Bornholm, Gdansk and southern Gotland Basins only)

Month	N	Vol (km^3)	Bornholm %
Feb	36	204 (20)	86 (0.03)
Mar	14	188 (37)	87 (0.04)
Apr	16	237 (35)	82 (0.04)
May	40	294 (37)	70 (0.04)
Aug	41	261 (37)	74 (0.04)
Oct	35	190 (20)	85 (0.03)

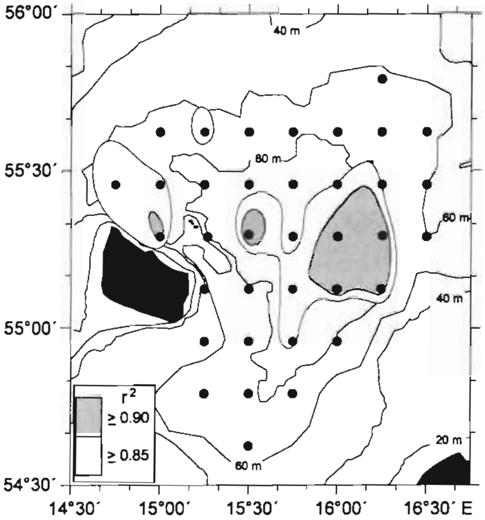

Fig. 5. R^2 values for cross-correlation between thickness of spawning layer and reproductive volume of cod based on a 36 station standard grid (1991 to 1996) in the Bornholm Basin

We repeated this analysis of variance using nonparametric statistical methods because some of the frequency distributions of the reproductive volumes departed from normal because of a high frequency of zero values. However, the results of 1-way nonparametric ANOVAs for differences between basins were similar to those of the parametric analysis (Kruskal-Wallis chi-square test: $p < 0.0001$ for sets of months with and without the central Gotland data).

The average monthly total reproductive volume in the Baltic Sea, as calculated from the LatFRI estimates for 1952 to 1992, and the fraction contained in the Bornholm Basin ranged from 188 to 294 km^3 and 70 to 87 %, respectively (Table 2). For the months of May and August, when estimates for the central Gotland Basin are available, the Bornholm Basin represents on average 70 to 74 % (standard error = 4 %) of the total reproductive volume in the Baltic Sea. For the other months, which exclude the contribution of the central Gotland Basin, the Bornholm Basin contains 82 to 87 % of the reproductive volume.

Assessment of horizontal homogeneity within a basin

The process of estimating the cod reproductive volume according to discrete values of the spawning-layer thickness can be facilitated by use of a simple-linear regression model. Fig. 5 shows the horizontal distribution of the R^2 values for the cross correlation between spawning layer thickness of a single station and corresponding cod reproductive volume based on the spatial coverage of 36 stations. Most of the locations displayed a high correlation of single-point observations of the spawning-layer thickness with horizontally integrated quantities of its water volume. For the northern part of the Bornholm Basin, the overall structure of the correlations did not change dramatically. It is apparent that highest values for R^2 occurred in the central deep part of the basin, whereas the correlations tend to decrease with decreasing water depth. Additionally, relatively high correlations were found for the Bornholm Gat region, i.e. the northwestern part of the study area. Generally, weaker correlations were found for the southern part of the Bornholm Basin with water depths <80 m.

Linear regression models for 4 locations in the central Bornholm Basin yielded correlations with $R^2 \geq 0.89$ (including the data from 1989 based on the reduced station grid: Fig. 6). For the observation dates in the period 1989 to 1996, the reproductive volume as estimated by basin-wide integration ranged from 8 km^3 (June 1989) to 229 km^3 (April 1994). The standard error of the basin-wide reproductive volume significantly increased with the mean (Fig 7). The corresponding maximum values for the thickness of the spawning layer varied considerably between the 4 stations. The highest value of 42 m was recorded in the center of the study area, followed by 33 m observed at a station located approximately 10 n miles further to the east. Close to the entrance to the Stolpe trench and ~12 n miles southeast from the central station, the maxima of the thickness of the spawning layer amounted to only 21 and 27 m, respectively. However, for all of these stations there was close correlation between the reproductive volume and the thickness of the spawning layer.

We therefore used one of these regression models (Fig. 6) to construct a time series of reproductive volumes from 1958 to 1996. The model we chose was that

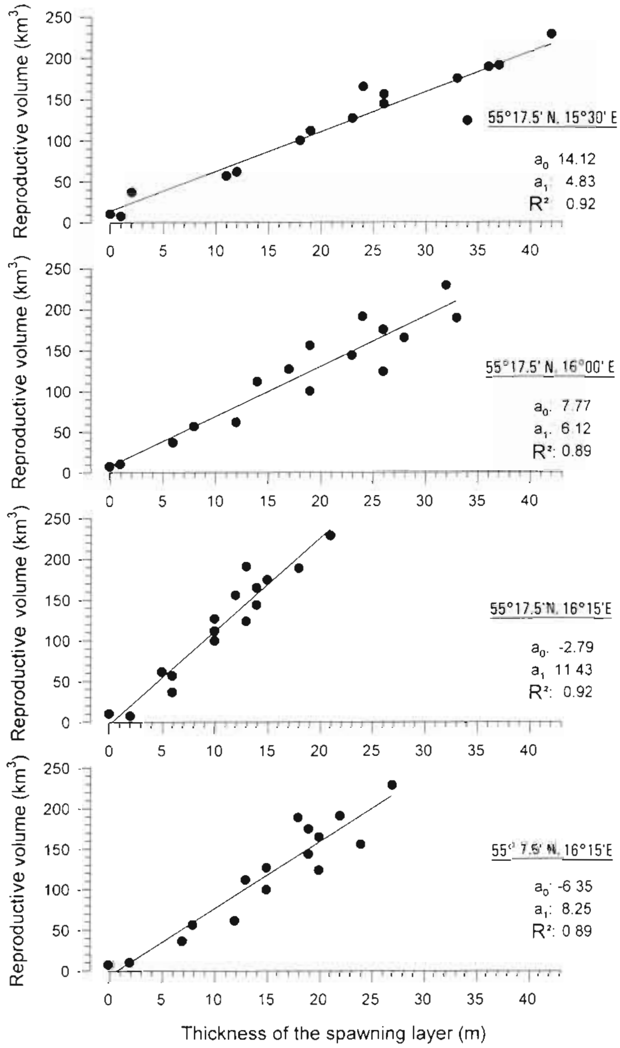

Fig. 6. Regression models for correlation of thickness of the spawning layer at 4 stations with basin-wide reproductive volume. (····) 95% confidence limits

for the station located at 55° 17.5' N, 16° 00' E. This station was the most frequently visited location (total number of observations = 466) during the recent decades; all single-point measurements were considered if they were <10 km from the nominal geographical position represented by the HELCOM international monitoring Stn BY5 (55° 15' N, 16° 00' E). The time series of reproductive volumes based on this station and calibration model were subsequently used for comparison with the Latvian estimates (see following subsection).

Intercomparison of 2 time series of reproductive volume for Bornholm Basin

The LatFRI time series spans the period 1952 to 1992 and has more observations (N = 246) than the Kiel

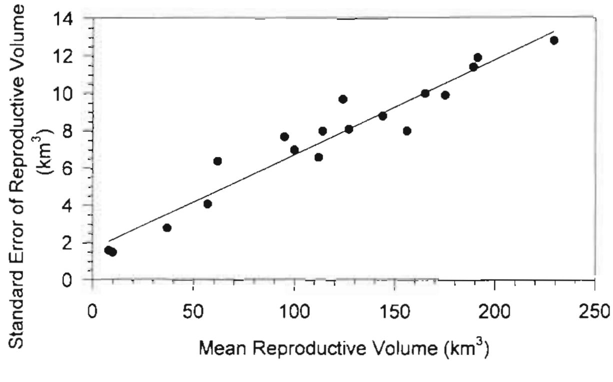

Fig. 7. Standard error of reproductive volumes estimated by objective analysis of a 36 station hydrographic grid for different mean levels of reproductive volume

series (N = 197), which began later (1958) and is ongoing (Table 1). Visual inspection of the time series plots suggests that the peaks and troughs in both series generally coincide (Fig. 3). However the Latvian series tends to have somewhat higher peaks than the Kiel series.

The frequency distribution of the values for each of the Bornholm Basin series suggests that the LatFRI estimates tend to be larger and that both series are slightly abnormal. A Student's *t*-test and variance-ratio test showed that the mean and variance of the LatFRI series were both significantly larger than the Kiel series (*t*-test for means: $p < 0.0001$; *F*-ratio test for variances: $p = 0.0009$). A 2-way ANOVA with month and institute as effects showed that only the institute effect was significant ($p < 0.0001$).

The Kiel estimates obtained by objective analysis are accompanied by estimates of their variability. A comparison of the variability of these estimates to the mean value shows that the variance increases significantly with the mean (Fig. 7). The Latvian estimates have no such error estimates.

Month-specific regression analyses between the 2 data series generally showed a strong correspondence between estimates (Table 3, Fig. 8). All regressions were highly significant ($p < 0.0001$) and the explained variation (R^2) was 44 to 82%. None of the slopes differed significantly from 1. However, the intercepts were close to being significantly different from zero for some months, and the intercept was highly significant when all months were combined for an overall analysis (Fig. 8). Intercept values ranged from –15.8 to 47.4 for individual months, and equalled 24.5 for the 'all months combined' model. The residual mean square error (a measure of how large an individual observation might deviate from the average pattern) for the 'all months combined' model is ca 43.6 km^3.

Using the month-specific models, we then updated the Latvian time series for the Bornholm Basin for the

Table 3. Statistical results of comparisons of 2 sets of reproductive volume (RV) estimates. Regression model fitted was $RV_{Latvia} = a + b \cdot RV_{Kiel}$. RMSE: residual mean square error of the observed estimates from predictions made by the regression model

Month	R^2	N	p	RMSE	a (SE)	p	b (SE)	p
Feb	0.80	31	<0.0001	34.9	19.8 (15.2)	0.2034	1.14 (0.11)	<0.0001
Mar	0.72	32	<0.0001	40.4	25.1 (16.7)	0.1422	1.04 (0.12)	<0.0001
Apr	0.44	32	<0.0001	65.6	47.4 (26.0)	0.0789	0.86 (0.18)	<0.0001
May	0.82	30	<0.0001	33.0	−15.8 (15.9)	0.3281	1.18 (0.10)	<0.0001
Aug	0.80	34	<0.0001	36.6	18.3 (13.9)	0.1953	1.08 (0.10)	<0.0001
Oct	0.73	22	<0.0001	39.4	36.2 (17.0)	0.0454	0.91 (0.12)	<0.0001
All months combined	0.68	181	<0.0001	43.6	24.5 (7.5)	<0.0001	1.02 (0.05)	<0.0001

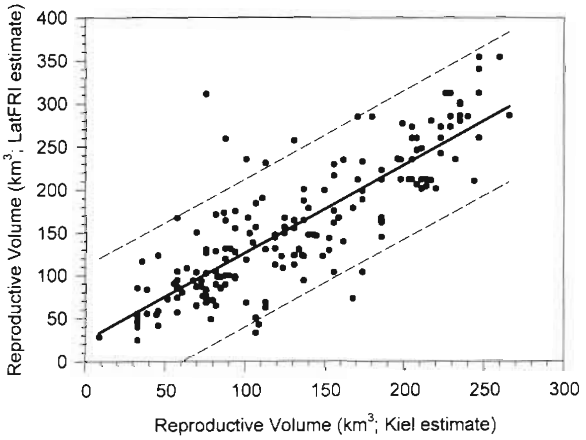

Fig. 8. Regression model comparing reproductive volumes in the Bornholm Basin for all months for which data were available during 1958–1992. Reproductive volumes were estimated by 2 different methods employing different input hydrographic datasets (see Table 3 for statistical results); (-----) 95% prediction limits

years 1993 to 1996 based on the measured Kiel estimates. The proximate LatFRI estimates for these years are shown in Fig. 3.

DISCUSSION

Time series development and methodological comparisons

Gadus morhua spawn in the Baltic Sea in well-defined areas, and the vertical distribution of their eggs is becoming increasingly better described (Wieland & Jarre-Teichmann 1997). In addition, the transport of eggs away from at least 1 of these spawning sites is likely to be limited under the most frequent hydrographic situations prevailing in the Baltic (Wieland 1995, Hinrichsen et al. 1997). In general, these 2 circumstances (known spawning site and high probability of geographic retention of the eggs) greatly facilitate operational definitions of the size and quality of the habitat occupied by fish eggs, particularly in comparisons with fish populations in areas where locations of spawning sites are variable (e.g. deYoung & Rose 1993, Anderson & Dalley 1997) or where boundaries surrounding the spawning site are much more dynamic (e.g. deYoung & Davidson 1994, Heath & Gallego 1997).

Our calculations and analyses show that under such circumstances it is possible to quantify the volume of water in which cod eggs can develop successfully in the Baltic Sea. These volume estimates should be considered as approximations because they assume 100 and 0% egg survival at oxygen concentrations above and below 2 ml^{-1}, respectively. In reality, laboratory experiments show that cod egg survival increases with increasing oxygen concentration in the range 2 to 5 ml^{-1}, and varies independently of oxygen concentration in the range 5 to 9 ml^{-1} (Wieland et al. 1994). Hence, our volume estimates probably overestimate the true volumes which ensure cod egg survival; in nature, therefore the volume of water that ensures cod egg survival with high probability will be somewhat smaller than the volumes estimated by our analyses.

Our analyses indicate that a carefully chosen monitoring site can represent conditions throughout an entire basin, at least for the purpose of estimating reproductive volumes. The locations of individual stations which gave the best correlation with the whole-grid volume estimates were those located in the central deep part of the basin. Correlations between reproductive volumes estimated by objective analysis using a 36-station grid as input and reproductive volumes estimated by extrapolating spawning layer thickness at 1 station throughout the basin were highly significant over a wide range of oxygen conditions in the Bornholm Basin. This relationship was used to develop an extended time series to enable comparison with an independent set of observations by Plikshs et al. (1993).

The comparison of the IfMK data with the independent set of observations developed by Plikshs et al.

(1993) showed that both series of estimates for the Bornholm Basin were similar, thereby giving confidence that both series reveal the major patterns of variability within the Bornholm Basin. In our analysis the difference in reproductive volume estimates between methods was similar for all ranges of reproductive volume (i.e. slope not significantly different from 1). We conclude that single-point estimates from the central deep part of the Bornholm Basin can produce reasonable estimates of the size and quality of habitat available for cod eggs. We also conclude that the strong relationship between the 2 series facilitates intercomparisons, the interpolation of missing values, and the construction of intact series into the future. Given the changes in sampling effort during the 1990s (see 'Introduction'), this could be useful for process-modelling studies of egg survival and recruitment.

The intercomparison of the 2 data series revealed some differences as a function of the time of year used in the comparison. For example, the explained variation was usually 70 to 80% for each month considered, except for April, when it was only 44%. We have no obvious explanation for the higher variability in April. In addition, within each monthly comparison there were some noticeable outliers. These could occur for example if the hydrographic data were collected at different times within the month and hydrographic conditions changed during the intervening period (e.g. initiation of an inflow from the western Baltic). Other sources of error contributing to the residual variability would include differences in the vertical positions of iso- and oxypycnals relative to the depth layers sampled during the research surveys.

The objective-analysis methodology used to produce the Kiel reproductive volume estimates from the 36-station grid yields a measure of reliability of the observed estimates. The standard error of a reproductive volume estimate obtained from objective analysis increases with the mean. The variance-mean relationship suggests that it may be necessary to sample at more stations when there are high oxygen levels in the basin, when the same degree of reproductive volume accuracy is desired. A larger spatial coverage under high oxygen conditions appears necessary to ensure that all oxygenated areas within the basin are sampled.

It is unclear whether the methodological comparisons for reproductive volume estimation in the Bornholm Basin would apply to the other spawning basins in the Baltic Sea. For example the environmental heterogeneity within each of the other basins may differ from that in the Bornholm Basin. Our analyses suggest that environmental heterogeneity in the Bornholm Basin is relatively low, since 1 carefully-chosen station can often approximate conditions throughout the basin. However, in either the Gdansk or Gotland Basins, conditions may be more heterogeneous for example because of differences in hydrographic processes and bottom topography (Feldman et al. 1996, Zezera & Zezera 1997). In such cases, single-station estimates of reproductive volume may be less representative of basin-wide conditions than is the case in the Bornholm Basin, and several stations might be necessary to provide reliable estimates. It would therefore be desirable to repeat the comparisons made in the Bornholm Basin in the remaining spawning areas.

Spatial and temporal heterogeneity in reproductive volumes

Our analyses of spatial and temporal heterogeneity of reproductive volumes quantify what many colleagues in the Baltic fisheries and oceanographic communities have recognized for years: conditions for successful cod-egg development are most likely to be found in the Bornholm Basin. Volumes in this basin were relatively high and less variable in comparison with volumes in the other basins. However, exceptions to this broad pattern do occur, particularly between years. For example, during the longest recorded period without a major inflow of North Sea water (1983 to 1993: Schinke & Matthäus 1998), reproductive volumes in this basin became very low. In addition, oxygen-renewal events (e.g. inflows) can rapidly and significantly improve conditions in all basins (Matthäus & Lass 1995).

These observations suggest that a detailed analysis of the temporal variability in reproductive volumes would be insightful. Some preliminary studies of the temporal variability in the Bornholm Basin using the Latvian time series (Plikshs et al. 1993) have shown that reproductive volumes vary seasonally (MacKenzie et al. 1996), and that these variations may be related to water temperature and oceanographic production processes (MacKenzie et al. 1996). The seasonal variations in reproductive volume are probably associated with seasonal variations in both oxygen concentrations (Matthäus 1978, Wieland 1995) and salinity, which is influenced by freshwater runoff to the Baltic (Viitasalo et al. 1995, Schinke & Matthäus 1998). In addition to seasonal variations in reproductive volumes, processes, such as eutrophication (Rahm et al. 1996, Wasmund et al. 1998), that operate at longer time scales could contribute to multi-annual variability. The present compilation of intercalibrated and validated data series will enable these variations to be investigated with greater confidence in the future.

The impact of the spatial and temporal heterogeneity in conditions at cod spawning sites on egg survival and recruitment may be significant. The temporal (interannual) variations in total reproductive volume appear to have a significant impact on recruitment, and it is inferred that this correlation is due to low egg survival when total reproductive volume is small (Plikshs et al. 1993, Sparholt 1996, Jarre-Teichman et al. in press). In addition, the spatial variations within a year will also probably be important. Jarre-Teichman et al. (in press) have noted that much (60 to 80%: ICES 1997) of the spawning stock was located in Subdivisions 26 and 28 in the early 1980s, when reproductive volumes in these same areas were essentially absent (Fig. 3), and that this may have contributed to the rapid decline in recruitment despite near-record high levels of spawning biomass. These observations suggest that heterogeneity at scales smaller than the entire management area or stock unit may influence egg survival or recruitment.

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Appendix 1. Raw reproductive volume (km^3) data used in intercalibration and comparative analyses; missing value code = −99

Table A1 Bornholm Basin. Latvian estimates from 1952–1992 (Plikshs et al. 1993). Years 1993–1996 based on prediction from Latvian-Kiel intercalibration model

Year	Feb	Mar	Apr	May	Aug	Oct
1952	325	259	247	284	272	195
1953	117	96	117	139	144	153
1954	215	231	246	276	276	224
1955	204	190	103	93.5	98.1	145
1956	162	155	103	133	149	190
1957	167	138	147	103	117	108
1958	112	93.5	67.2	59	39.7	55.1
1959	175	161	147	147	298	198
1960	167	147	103	234	235	205
1961	284	339	339	259	232	216
1962	187	130	122	122	150	86.5
1963	89	75.5	48.5	115	167	234
1964	210	203	164	178	162	241
1965	222	211	167	161	93.1	162
1966	103	93.4	126	146	138	199
1967	171	190	259	284	144	167
1968	173	99.5	75.5	70.7	43.7	85
1969	234	200	211	259	272	211
1970	229	234	284	200	167	155
1971	184	116	104	79.7	48.6	126
1972	96	235.2	311	353	285	211
1973	164	231	279	245	144	224
1974	353	311	209	179	257	235
1975	83	67.8	86.5	64.3	38	28.1
1976	311	211	247	247	285	320
1977	284	272	311	234	139	104
1978	175	190	143	122	119	134
1979	102	84.5	72.3	68.2	108	147
1980	272	300	279	211	200	259
1981	127	131	67.8	64.9	33.3	51.8
1982	94	73.6	86.3	84.6	89.8	91.1
1983	259	284	234	144	104	130
1984	164	130	112	118	156	131
1985	147	149	164	123	84.4	98.1
1986	64	56.6	71.9	103	156	131
1987	58	82.9	89	97.6	99.5	108
1988	150	123	128	98.1	24.4	46.8
1989	54	82.2	123	42.5	55.1	27.4
1990	16	46.3	41.17	108	24.4	50.1
1991	32	129	167	188	178	157
1992	234	222	211	211	62	32.9
1993	-99	-99	198	179	222	-99
1994	-99	-99	244	210	187	-99
1995	-99	-99	171	116	80	-99
1996	-99	-99	101	96	141	133

Table A2. Bornholm Basin. Kiel estimates (Hinrichsen & Wieland 1996). During 1993, 1995 and 1996 there were no August estimates; data analyses used values for July instead

Year	Feb	Mar	Apr	May	Jul	Aug	Sep	Oct
1952	-99	-99	-99	-99	-99	222	-99	-99
1953	-99	-99	-99	-99	-99	-99	-99	-99
1954	-99	-99	-99	-99	-99	198	-99	-99
1955	-99	-99	-99	-99	-99	82	-99	-99
1956	-99	130	-99	-99	-99	102	-99	-99
1957	-99	-99	-99	-99	-99	-99	-99	-99
1958	130	136	-99	-99	-99	32	-99	38
1959	155	155	142	118	-99	234	-99	173
1960	124	139	173	-99	-99	195	-99	207
1961	179	-99	246	246	-99	173	-99	155
1962	136	133	122	136	-99	69	-99	72
1963	87	75	78	-99	-99	101	-99	204
1964	216	213	136	139	-99	-99	-99	222
1965	185	185	185	185	-99	72	-99	-99
1966	69	67	75	144	-99	104	-99	149
1967	81	110	87	239	-99	185	-99	57
1968	86	89	73	79	-99	32	-99	32
1969	197	136	202	204	-99	204	-99	204
1970	155	161	170	210	-99	124	-99	93
1971	106	35	57	60	-99	-99	-99	-99
1972	93	100	75	259	-99	234	-99	210
1973	185	112	216	207	-99	118	-99	-99
1974	246	246	243	-99	-99	130	-99	-99
1975	75	75	57	81	-99	-99	-99	8
1976	228	197	-99	210	-99	265	-99	-99
1977	-99	222	225	-99	-99	161	-99	-99
1978	93	-99	152	148	-99	87	-99	-99
1979	75	-99	167	112	-99	123	-99	-99
1980	228	234	234	213	-99	219	-99	207
1981	93	87	100	69	-99	-99	-99	32
1982	57	57	69	57	-99	55	-99	-99
1983	222	228	231	118	-99	81	-99	75
1984	130	112	118	100	-99	124	-99	90
1985	118	124	87	135	-99	84	-99	-99
1986	69	57	51	155	-99	106	-99	118
1987	45	38	81	84	-99	87	-99	63
1988	124	130	81	93	-99	32	-99	-99
1989	44	75	45	108	-99	32	-99	-99
1990	-99	32	45	63	-99	-99	-99	106
1991	-99	152	158	173	-99	167	-99	-99
1992	-99	-99	-99	170	-99	112	-99	106
1993	-99	-99	175	165	189	-99	-99	-99
1994	-99	-99	229	191	156	169	-99	-99
1995	-99	-99	144	112	57	-99	37	37
1996	-99	-99	62	95	114	-99	-99	106

Table A3. Gdansk Basin. Latvian estimates from 1952–1992 (Plikshs et al. 1993). Values for 1993 and 1994 are estimated from Feldman et al. (1996)

Year	Feb	Mar	Apr	May	Aug	Oct
1952	-99	-99	14	0	32.9	-99
1953	-99	-99	-99	84.2	19.2	-99
1954	-99	-99	-99	45.2	21.6	-99
1955	40.8	-99	-99	22.3	0	-99
1956	19.8	-99	-99	50	9.8	-99
1957	15.6	-99	-99	15.5	0	0

Table A3 (continued)

Year	Feb	Mar	Apr	May	Aug	Oct
1958	0	–99	–99	0	0	0
1959	0	–99	–99	0	0	22
1960	5	–99	9	5.07	54.4	40
1961	77	–99	–99	125	110	100
1962	10	–99	–99	0	14.3	0
1963	4	–99	–99	0	0	0
1964	54	–99	–99	104	65.2	54
1965	132	–99	–99	98.8	16.2	41
1966	19	–99	–99	36	26.3	36
1967	77	–99	–99	110	57.3	0
1968	0	–99	–99	0	0	0
1969	125	–99	65	90.1	99.7	40
1970	71	75	88	101	22.2	22
1971	–99	–99	–99	0	16.4	0
1972	0	–99	–99	110	104	0
1973	0	0	–99	80.3	22.5	15
1974	0	–99	0	0	36	0
1975	0	0	0	0	0	0
1976	–99	83	22	70.9	49.9	147
1977	54	90	65	51.5	82.4	31
1978	0	–99	–99	65.3	30.4	20
1979	52	–99	–99	13.3	0	38
1980	21	–99	22	58.7	85.7	26
1981	0	–99	–99	0	0	0
1982	0	0	–99	0	0	0
1983	19	32	23	20.2	8.5	0
1984	0	0	–99	0	7.8	12
1985	10	40	25	16.4	5.4	0
1986	16	0	0	0	0	0
1987	16	0	0	0	7.8	0
1988	0	0	0	0	0	0
1989	0	0	0	0	0	0
1990	0	0	0	0	0	0
1991	0	–99	–99	0	0	0
1992	0	–99	–99	0	0	–99
1993	–99	–99	–99	41	59	–99
1994	–99	–99	–99	67	59	–99
1995	–99	–99	–99	–99	–99	–99
1996	–99	–99	–99	–99	–99	–99

Table A4. Southern Gotland Basin. Latvian estimates from 1952–1992 (Plikshs et al. 1993). Estimates for 1993–1996 from Plikshs (1996, unpubl.)

Year	Feb	Mar	Apr	May	Aug	Oct
1952	–99	–99	69	–99	139	–99
1953	–99	–99	–99	161	83.1	–99
1954	–99	–99	–99	114	132	–99
1955	108	–99	–99	83.1	32.5	–99
1956	24	–99	–99	101	13.8	0
1957	30	–99	–99	26.4	22.7	0
1958	0	–99	–99	0	0	0
1959	0	–99	–99	0	0	0
1960	34	57	57	43.9	78.5	71
1961	119	–99	–99	41.4	0	0
1964	103	103	108	92.4	13.2	76
1965	103	125	125	14.9	57	100
1966	0	15	54	150	4.3	0
1967	0	0	0	18.7	0	0

Table A4 (continued)

Year	Feb	Mar	Apr	May	Aug	Oct
1968	0	0	0	0	0	0
1969	0	0	78	41.4	48.7	71
1970	26	61	45	119	92.4	97
1971	0	0	0	0	0	0
1972	0	0	0	18.7	65.1	131
1973	0	0	0	18.7	31.6	0
1974	0	92	61	73.9	0	0
1975	0	0	0	0	0	0
1976	15	38	69	103	87.8	89
1977	92	97	108	83.1	92.4	100
1978	38	108	92	92.4	69.3	16
1979	0	8	41	41.4	0	0
1980	0	0	103	108	87.7	35
1981	0	0	0	0	0	0
1982	0	0	0	0	0	0
1983	0	32	35	38	18.7	18
1984	0	19	5	34.6	8.5	85
1985	8	11	6	9.76	4.8	3
1986	0	7	0	8.48	0	0
1987	0	0	0	0	0	0
1988	0	0	0	0	0	0
1989	0	0	0	0	0	0
1990	0	0	0	0	0	0
1991	0	0	0	0	0	0
1992	0	−99	−99	0	0	0
1993	0	−99	−99	0	0	0
1994	7	−99	−99	54	2	0
1995	−99	−99	−99	0	0	0
1996	−99	−99	−99	−99	−99	−99

Table A5. Central Gotland Basin. Latvian estimates from 1952–1992 (Plikshs et al. 1993). Estimates for 1993–1996 from Plikshs (1996, unpubl.)

Year	May	Aug	Year	May	Aug
1952	552	563	1975	51.2	0
1953	559	24.7	1976	153	323
1954	433	578	1977	93	255
1955	545	277	1978	0	0
1956	0	0	1979	0	0
1957	0	0	1980	0	0
1958	0	0	1981	0	0
1959	0	0	1982	0	0
1960	0	72.2	1983	0	49
1961	157	0	1984	0	120.9
1962	52.7	0	1985	5.92	35.7
1963	0	0	1986	0	0
1964	327	314	1987	0	0
1965	0	0	1988	0	0
1966	0	0	1989	0	0
1967	0	0	1990	0	0
1968	0	0	1991	0	0
1969	0	0	1992	0	0
1970	0	0	1993	0	0
1971	0	0	1994	67	229
1972	153	0	1995	0	0
1973	0	0	1996	0	0
1974	0	0			

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